TEMPORAL PATTERNS OF MIGRATION, MOLT, AND FAT STORAGE AMONG HIGH-LATITUDE PASSERINE MIGRANTS

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A

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ABSTRACT

Aspects of migration, fattening, and molt in trans-continental passerine migrants were examined during spring and autumn migration in Fairbanks, Alaska (64°50' N, 147°50' W). From 1992-1998, 25,718 birds of 18 species were banded. Based on median dates of spring and autumn passage, species-level estimates of the duration of breeding range occupation ranged from 48 to 129 days. Adults departed significantly later than immatures in 11 of the 18 species examined and significantly earlier than immatures in only one species, the Alder Flycatcher. Adults had significantly higher fat scores than immatures in most species, but these differences were attributable to the influence of ambient temperatures, length of preceding night, and the time of day the bird was captured. Adults of many species overlapped the final stages of the prebasic molt with autumn migration, and individuals that did so had less stored fat than those that were not molting.

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INTRODUCTION

The high latitudes of North America support a diverse avifauna, because during the summer months the region is characterized by a nutrient-rich environment, an extended photoperiod, and a hospitable climate. But summer at high latitudes is brief. The birds that breed in this region must time their arrival and departure within the brief period of available resources. We examined the duration of breeding range occupancy of long-distance passerine migrants in Fairbanks, Alaska, near the northwestern extremes of the continental landmass. We also examined the timing of prebasic molt in passerine migrants to determine whether species overlap the timing of migration and molt, two energetically demanding processes. We expected that the likelihood that species may overlap these life-history events would be highest in regions where summer is briefest. We also examined seasonal variation in fat storage in migrants during spring and autumn migration, and during the molt period, to determine the variation in body condition in passerine migrants during the time they occupy their breeding range.

CHAPTER 1 - TIMING OF BREEDING RANGE OCCUPANCY AMONG HIGH LATITUDE PASSERINE MIGRANTS

ABSTRACT

The brief subarctic summer limits the time available for birds to complete their reproductive activities, yet the time required by high-latitude passerine migrants is not well known. Our analyses examined the timing of spring and autumn migration among 18 passerine species to obtain indirect estimates of the time they occupy their breeding ranges in northwestern North America. From 1992 to 1998, the Alaska Bird Observatory banded 25,718 individuals of these 18 species in Fairbanks, Alaska (64°50' N, 147°50' W). Among the migrants examined, the estimated number of days that species were present in Interior Alaska ranged from 48 days for adult Alder Flycatchers (*Empidonax alnorum*) to 129 days for adult American Robins (*Turdus migratorius*). Adults departed significantly later in autumn than immatures in 11 of the 18 species and significantly earlier than immatures in only one species, the Alder Flycatcher. Breeding range occupancy of Nearctic-Neotropic migrants occurs in this region within the range of average frost-free temperatures in Fairbanks, Alaska, and is significantly shorter in duration than among Nearctic-Nearctic ("short-distance") migrants at this latitude.

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INTRODUCTION

The high latitudes of North America support a diverse avifauna, because during the summer months the region is characterized by a nutrient-rich environment, an extended photoperiod, and a hospitable climate. But summer at high latitudes is brief. For example, the frost-free period at Fairbanks, Alaska averaged 105 days (20 May to 2 September) during 1905-1999 (National Weather Service data). Birds that migrate to Alaska are therefore under greater temporal pressure to complete their breeding season activities (i.e., territory and mate acquisition, nest building, egg laying, incubation, rearing of nestlings, post-fledgling care, and molt) than birds breeding at lower latitudes.

For numerous reasons, the total amount of time passerines occupy their breeding ranges is not well documented. First, few studies of passerines at high latitudes have been conducted from the beginning through the end of the breeding season (but see Williamson et al. 1966, Rimmer 1988). Second, studies that have examined breeding chronology at northern locations may not accurately document departure from the breeding grounds because of small sample sizes and local postbreeding dispersal. In some passerines, postbreeding dispersal to molt and build up energy stores occurs prior to migration (Stewart 1973, Rappole and Ballard 1987, Rimmer 1988). The timing of departure from a breeding territory, therefore, does not necessarily represent departure from the breeding grounds.

Studies that sample migrant passage during spring and autumn provide an indirect measure of time spent on the breeding grounds. The accuracy of such a measure increases with proximity to a population's breeding area. All previous studies of the

timing of passerine migration in North America have occurred south of 45° N (Winker et al. 1992). Studies at lower latitudes have documented the timing of spring or autumn migration at various migratory stopover sites in North America (Francis and Cooke 1986, Hagan et al. 1991, Hussel 1991a, 1991b, Winker et al. 1992, and Woodrey and Chandler 1997). These studies can document passage dates, but their location at lower latitudes in relation to the breeding ranges of high-latitude populations gives only a maximum estimate of the duration of breeding ground occupancy for many migrants.

We sampled migrants near the northern and western limits of the their migration routes during spring and autumn. Our objective here is to examine the timing of passage at the species level in this region to obtain indirect estimates of the time birds occupy their breeding ranges in the northwestern extreme of North America. Additionally, we answer the following questions: (1) Is there among-year variation in the timing of spring and autumn passage? (2) Do Nearctic-Neotropic migrants differ from Nearctic-Nearctic ("short-distance") migrants in the timing of breeding range occupancy?

Study Area and Methods

The study area is located in Fairbanks, Alaska (64°5' N, 147°5' W), approximately 10 km from the confluence of the Chena and Tanana rivers (elevation 130 m). The Tanana Valley is a well-documented migration corridor for many species of birds, including Sandhill Cranes (*Grus canadensis*; Kessel 1984), many species of raptors (McIntyre and Ambrose 1999), waterfowl, shorebirds, and passerines (Cooper and Ritchie 1995).

The study site, at Creamer's Field Migration Station (CFMS), encompasses approximately 20 ha of the southwestern portion Creamer's Field Migratory Waterfowl Refuge (731 ha). It is owned by the State of Alaska and operated by the Alaska Department of Fish and Game. The northern portion of CFMS is dominated by mature willow (*Salix* spp.) and paper birch (*Betula papyrifera*) bordering a seasonally flooded wetland dominated by sedges (*Carex* spp.) and one grass species (*Calamagrostis canadensis*). The central section of the study area is characterized by late successional white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The southern portion of the study area has trembling aspen (*Populus tremuloides*), balsam poplar, and willow growing near a large agricultural field. Except for the agricultural field, this mosaic of habitat types is representative of the habitat types occurring in the floodplains of the boreal forest of Interior Alaska.

A standardized mist-netting protocol was conducted at CFMS from 1992-1998 using an array of 22-50 standard mist nets (30 mm mesh, 2.6 m x 12 m). The nets were arranged in a north-south direction, perpendicular to the Tanana Valley migration corridor. Nets were operated daily from 0600 to 1300 during spring migration (25 April-15 June). During autumn migration (15 July-30 September) nets were opened at approximately sunrise and closed seven hours later. Sampling at the ends of both seasons (10-15 June and 25-30 September) was limited to every other day. Nets were closed during inclement weather. Fewer nets were operated in 1992, 1997, and 1998 compared with other years (Table 1.1). Also, nets were not operated between 17 July and 2 August 1992.

Birds were banded with United States Fish and Wildlife Service bands, and data were collected to determine age (autumn only, using degree of skull ossification), and breeding condition (spring only, scoring incubation patches in females and cloacal protuberances in males). During autumn migration, estimates of the percentage of juvenal plumage were recorded for individual first-year birds using four categories: no juvenal plumage, less than 1/3 of the body in juvenal plumage, 1/3-2/3 of body in juvenal plumage, and greater than 2/3 of the body in juvenal plumage.

We assumed that only a small proportion of birds included in these analyses were potentially breeders for two reasons. First, we excluded known local breeders from the analyses based on the following criteria: females with incubation patches, individuals captured more than seven days from first capture, and birds captured in one season and recaptured in another. First captures of individuals were also removed if they were later recaptured with breeding characteristics. We also excluded first-year birds with more than 30% of their body in juvenal plumage, as we considered them nonmigratory at that time. Finally, for most species the number of individuals captured late in the spring netting period (5-15 June) and early in the autumn netting period (15-25 July) represented less that 2% of the total birds included in the analysis (Appendices 1.1 and 1.2). Therefore, any local breeders that were possibly not removed could not have a profound influence on our estimates of the timing migratory movements at the species level.

We defined Nearctic-Neotropic migrants as those species that breed north of the Tropic of Cancer and primarily winter south of that line (Rappole et al. 1983). We defined Nearctic-Nearctic migrants as those species with breeding and wintering ranges

primarily north of the Tropic of Cancer. These species are often categorized as "short-distance" migrants.

An estimate of time spent on the breeding grounds was obtained from the difference between the median dates of spring and autumn passage. To ensure that independent captures of birds were used for the analyses of timing of migration, we used only initial captures of individuals (i.e., all subsequent captures of individuals were eliminated from the analyses). We used first capture of individuals in autumn, rather than last capture, to ensure that our study could be compared with previous studies on the timing of migrant passage (e.g., Francis and Cooke 1986, Hagan et al. 1991, Hussel 1991a, 1991b, Winker et al. 1992, Woodrey and Chandler 1997).

We did not standardize the number of birds captured by unit of netting effort for two reasons. First, net hours were uniformly distributed among days when all years were combined during spring (Kolmonogrov-Smirnov test, *KS*-test, for goodness of fit to a uniform distribution, $Dmax = 0.08$, $N = 68{,}196$, $P > 0.10$) and autumn (*KS*-test, $Dmax = 0.07$, $N = 87{,}627$, $P > 0.10$). Second, standardizing captures by unit of netting effort can impart bias by artificially inflating or deflating sample sizes.

The difference in the duration of time that Nearctic-Nearctic and Nearctic-Neotropic migrants occupy their breeding ranges was examined using the Mann-Whitney *U*-test. We did not adjust our analyses for phylogenetic relationships, because closely related taxa often respond differently to migratory pressures, i.e., migration systems often are not influenced by common ancestry (e.g., *Catharus* thrushes; Winker 2000). We examined the differences between age-classes in the distributions of captures using the

Mann-Whitney *U*-test. Differences in timing of migration between age classes could affect species-level estimates of the median date of autumn passage, because first-year birds comprised the majority of autumn captures at this study site. Among-year differences within seasons were examined for those species in which at least 5 individuals were captured each spring or autumn (adults only) using the Kruskal-Wallis one-way analysis of variance. Because each of these tests was conducted on sixteen species, we used Bonferroni corrections to decrease the probability of Type I statistical errors. Therefore, *P*-values less than 0.05/18 species (0.003) were considered significant.

Weather data were collected at the Fairbanks International Airport and provided by the National Weather Service, Fairbanks office.

RESULTS

From 1992-1998, staff of the Alaska Bird Observatory accumulated 68,196 net hours during spring and 88,627 net hours during autumn (Table 1.1). During these seven years, 31,698 birds of 58 species were banded. We examined the timing of passage of 25,718 individuals among 18 passerine species. Judging from capture distributions (Appendix 1.1 and 1.2), the netting periods spanned the entire spring and autumn migration periods for all species analyzed except Alder Flycatcher (*Empidonax alnorum*). Spring netting was truncated shortly after peak passage of this species. Therefore, for this species, median spring passage dates may be slightly later than presented here.

Differential timing between age classes in autumn--

There were significant differences in median dates of autumn passage between adults and immatures in 11 of 18 species (Table 1.2). The Alder Flycatcher was the only

species in which the departure date of adults preceded that of immatures ($Z = 3.73$, $P < 0.003$); this difference averaged 13 days (Table 1.2). In Ruby-crowned Kinglets (*Regulus calendula*), Swainson's Thrushes (*Catharus ustulatus*), American Robins (*Turdus migratorius*), Orange-crowned Warblers (*Vermivora celata*), Yellow-rumped Warblers (*Dendroica coronata*), Yellow Warblers (*Dendroica petechia*), Blackpoll Warblers (*Dendroica striata*), Wilson's Warblers (*Wilsonia pusilla*), American Tree Sparrows (*Spizella arborea*), White-crowned Sparrows (*Zonotrichia leucophrys*), and Dark-eyed Juncos (*Junco hyemalis*) immatures preceded adults (Table 1.2). The largest significant age-related difference in passage dates occurred in Wilson's Warblers and Dark-eyed Juncos; in both species, adults migrated 13 days later than immatures. In 6 of 18 species there were no differences detected between adults and immatures in median dates of passage. Because there were significant age-related differences in departure dates in several species we examined, and because inference of this departure is conflated by large numbers of immatures (lowering accuracy; Table 1.2), we eliminated immatures from subsequent analyses for all species.

Duration of breeding range occupancy--

The length of time that adults occupied their breeding ranges was lower for Nearctic-Neotropic migrants ($n = 12$) than for Nearctic-Nearctic migrants ($n = 6$) (Mann-Whitney $U = 71.0$, $P < 0.05$; Table 1.2). The mean period of breeding range occupancy for all Nearctic-Neotropic migrants was 90.6 days (SE = 15.1 days), or less than 25% of the annual cycle. Nearctic-Nearctic migrants averaged 119.8 days (SE = 8.4 days), or 33% of the annual cycle.

The estimated number of days that adults were present in Interior Alaska ranged from 48 days for Alder Flycatchers to 129 days for American Robins (Table1.2). The 48 days between the median dates of spring and autumn passage of Alder Flycatchers suggest that the northern Alaskan populations of this species spend, at most, just 13% of the annual cycle on their breeding range. The next-briefest times between median dates of spring and autumn passage occurred in Yellow Warblers, Hammond's Flycatchers (*Empidonax hammondii*), and Northern Waterthrushes (*Seiurus noveboracensis*), which spent 84, 86, and 86 days, respectively, on their breeding ranges, or approximately 23% of the annual cycle.

Among-year variation in timing of passage--

Significant among-year variation in spring passage dates was detected in only one of five species examined, the Yellow-rumped Warbler ($KS = 19.22$, $df = 6$, $P < 0.01$; Appendix 1.1). No difference in median dates of spring passage was detected in Swainson's Thrush, American Robin, Orange-crowned Warbler, and Wilson's Warbler (Appendix 1.3). No significant differences were detected among years in timing of autumn passage for 7 species examined (adults only; Appendix 1.4).

DISCUSSION

Differential timing between age classes--

Our analyses showed immatures departing prior to adults in seven species. The differences between age classes observed in some species may be explained by the timing of molt in the adults, which, unlike immatures, replace their flight feathers in autumn.

Differences in timing of passage between adult and immature Swainson's Thrushes were not detected at study sites in Long Point, Ontario, western Pennsylvania, or coastal Alabama in 1990 (Woodrey and Chandler 1997). The same was true for 1991, with the exception of Long Point, where the median date of passage of adults was significantly earlier than immatures (Woodrey and Chandler 1997).

The Alder Flycatcher was the only species in our study in which adults preceded immatures in autumn migration. We estimated that adult Alder Flycatchers departed 13 days earlier than immatures of this species, which is similar to previous observations by Hussel (1991b), who found a 14 day difference between passage of adults and immatures at Long Point, Ontario. The lack of molt in adults of this species prior to autumn migration (Dwight 1900) probably accounts for this difference.

Temporal compression of breeding-season activities--

Studies at lower latitudes have suggested that the duration of the breeding season for some Nearctic-Neotropic migrants is brief. Winker et al. (1992) studied passerine migration in Minnesota at approximately 45°N and concluded that many species spend less than 30% of their annual cycle on their breeding grounds. In this study, at 64°N and much nearer to the final destination of high-latitude migrants, we estimated that populations of Nearctic-Neotropic migrants captured at our study site occupy their breeding ranges for less than 25% of their annual cycles, and that Nearctic-Nearctic migrants average 33% of their annual cycles on these high-latitude breeding ranges.

The 48 day difference between median spring and autumn passage dates of Alder Flycatchers in Interior Alaska suggests that this species spends just 13% of its annual

cycle on these northern breeding grounds. The actual duration of time this species occupied the breeding range is likely somewhat less than the 48-day estimate because the species was still likely migrating through this study site when the spring ended. This is the briefest duration of breeding range occupancy yet documented for a population or species of migratory passerine. In comparison, a lower-latitude study estimated 73 days between median dates of spring and autumn passage of Alder Flycatchers (adults only) (Hussel 1991a,b).

We estimated that some Alaska populations of Yellow Warblers occupied their breeding range for 84 days, which suggests decided compression when compared with the 104 days estimated to be required to accomplish breeding season activities in Delta Marsh, Manitoba, at 50°N (Busby and Sealy 1979). More northerly studies of Yellow Warblers indicate that breeding activities at high latitudes are indeed compressed. At Churchill, Manitoba (Briskie 1995) and James Bay, Ontario (Rimmer 1988), Yellow Warblers initiated clutches 12-30 days after arrival (Briskie 1995); the laying of 4-5 eggs must take at least 4-5 days; incubation took 11-13 days (Rimmer 1988, Briskie 1995); fledging took place 8-10 days after hatching (Briskie 1995); and adult prebasic molt began 8-12 days after young were fledged and lasted 35-45 days (Rimmer 1988). This provides an estimate of 79-115 days required by Yellow Warblers for breeding range activities at other high-latitude sites, and is in rough accordance with our estimate of 84 days for the completion of breeding season activities for this species in Interior Alaska.

We attempted to compare our estimates of breeding range occupancy with the duration of life-history events during the breeding season for other species, but found too

few relevant data. Although there are species-specific records for the duration of incubation and nestling stages, there are few records of the duration of territory and mate acquisition, nest building, parental care after fledging, and molt. Our indirect estimates of the duration of the breeding season in Interior Alaska are almost certainly less than the time spent by many species or populations at lower latitudes, especially among those species known to complete two clutches at lower latitudes, such as Savannah Sparrows in Nova Scotia (Welsh 1975) and Blackpoll Warblers in New Brunswick (Eliason 1986). In Nova Scotia, incubation in Savannah Sparrows took 12 days, the nestling stage was 9 days, and parental care after fledging was 28-35 days, resulting in a requirement of 49-56 days for a single clutch (Welsh 1975). The full completion of two clutches in Alaska therefore seems impossible for this species, because it is only present in Alaska for approximately 92 days and adults must also undergo a complete prebasic molt.

Among-year variation in timing of passage--

Hagan et al. (1991) found that species wintering in the Neotropics showed significantly less within-year and among-year variation in the timing of spring migration than species wintering in temperate regions. We thus expected higher among-year variation in median dates of passage among Nearctic-Nearctic migrants than among Nearctic-Neotropic migrants, particularly in spring, because the timing of arrival on the breeding grounds could be influenced by many factors, such as weather. However, among-year variation in spring passage was detected in only one of five species examined, the Yellow-rumped Warbler. This species shows facultative nonbreeding migration, and overwintering locations vary with local food availability (Terrill and

Ohmart 1984). It is likely that the median date of spring passage for this species in Alaska depends on how far north individuals overwintered in any particular year. The lack of variation among other species that we examined suggests that they may not vary the timing of migration based on environmental cues, as has been suggested for some North American species wintering in the Temperate Zone (Hagan et al. 1991). There were no significant among-year differences in median autumn passage dates in 16 species examined, suggesting that timing of departure from the breeding grounds at these latitudes is not a very flexible event in the populations examined.

Timing of breeding range occupancy--

The latest date on which freezing temperatures have occurred in spring in Fairbanks since 1905 was 13 June (1922), and the earliest date of freezing temperatures in autumn was 3 August (1944). In this region, Alder Flycatchers arrive near the record last date of frost in spring and leave before the record first date of frost in autumn (Table 1.2). This is probably not a coincidence. It is well known that flying insect availability is negatively affected by frosts, and this would seem to provide strong selection against the Alder Flycatcher's occupation of its breeding grounds during times of potential frost. Other insectivorous birds probably forage on a more diverse prey base when flying insects are not available and are therefore occasionally able to withstand early and late frosts in extreme years.

Nearctic-Nearctic migrants averaged 119.8 days between spring and autumn median dates of passage, and Nearctic-Neotropic migrants averaged 90.6 days. All but one Nearctic-Neotropic species, the Yellow-rumped Warbler, appeared to time their

arrivals and departures within the long-term average of 105 days of frost-free temperatures in Fairbanks, Alaska. Nearctic-Neotropic migrants rely primarily on insects for food, and are likely to be present as this resource waxes, becomes abundant, and then wanes. The one exception, the Yellow-rumped Warbler, may have more varied food habits than other species examined (Hunt and Flashpohler 1998). Conversely, most of the Nearctic-Nearctic species we studied rely on a seed- or fruit-dominant diet in winter, accounting for their ability to be present during periods of frost and indeed frozen conditions. Further, Nearctic-Nearctic migrants may be better adapted to adverse climatic conditions, which they may also experience on wintering areas. In northwestern North America, Nearctic-Neotropic migrants tightly time their breeding range occupancy to fit within the summer frost-free period, and complete their annual reproductive cycle in a brief temporal window.

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Table 1.1. Net hours of operation and total days of netting in spring and autumn at Creamer's Field Migration Station in Fairbanks Alaska (1992-1998).

Year	Spring		Fall	
	Net Hours	Days	Net Hours	Days
1992	6,903	42	5,822	46
1993	10,552	43	13,472	50
1994	11,252	41	13,935	52
1995	12,731	45	13,944	57
1996	12,411	44	14,985	57
1997	7,548	42	14,617	66
1998	6,800	39	11,853	54
Total	68,196	296	88,627	382

Table 1.2. Timing of migration (median Julian dates of passage) during spring and autumn, and differences between adults and immatures (results from Mann-Whitney *U*-Tests) during autumn among passerine species in Fairbanks, Alaska (1992-1998).

		Spring Migration			Autumn Migration							
					Adults			Immatures				
Species	Status	n	Range	Date[A]	n	Range	Date[A]	n	Range	Date[A]	*Z*	Days[B]
Alder Flycatcher (*Empidonax alnorum*)	L	39	154-167	161	83	196-237	209	342	204-256	222	8.81**	48
Hammond's Flycatcher (*Empidonax hammondii*)	L	58	115-166	138	19	198-259	224	226	196-249	216	1.66	86
Ruby-crowned Kinglet (*Regulus calendula*)	S	46	116-143	130	107	226-269	253	846	198-273	245	4.32**	123
Gray-cheeked Thrush (*Catharus minimus*)	L	102	135-159	144	45	199-265	242	187	211-261	239	2.76*	98
Swainson's Thrush (*Catharus ustalatus*)	L	283	132-159	145	82	224-270	240	675	198-268	232	7.24**	95
American Robin (*Turdus migratorius*)	S	217	121-167	137	77	235-271	266	198	205-272	249	6.66**	129
Orange-crowned Warbler (*Vermivora celata*)	L	252	130-164	143	582	196-266	245	3,378	196-270	237	8.63**	102
Yellow-rumped Warbler (*Dendroica coronata*)	L	539	117-163	136	376	208-268	244	5,663	196-266	234	5.49**	108
Yellow Warbler (*Dendroica petechia*)	L	149	135-167	151	94	199-264	235	734	196-260	227	7.42**	84
Blackpoll Warbler (*Dendroica striata*)	L	69	135-160	142	37	223-266	236	359	209-256	231	4.07**	94
Northern Waterthrush (*Seiurus noveboracensis*)	L	210	133-159	143	12	221-237	229	221	197-252	227	1.15	86
Wilson's Warbler (*Wilsonia pusilla*)	L	242	129-162	144	90	207-271	242	822	198-271	229	9.58**	98
American Tree Sparrow (*Spizella arborea*)	S	88	117-153	131	501	236-271	257	3,224	224-274	256	3.53**	126
Savannah Sparrow (*Passerculus sandwichensis*)	L	197	126-167	143	30	198-268	235	536	197-270	231	2.55*	92
Fox Sparrow (*Passerella iliaca*)	S	48	115-147	131	64	228-264	247	221	199-269	244	2.44*	116
Lincoln's Sparrow (*Melospiza lincolnii*)	L	71	124-167	139	60	196-269	235	1,259	196-273	229	1.28	96
White-crowned Sparrow (*Zonotrichia leucophrys*)	S	93	123-156	135	37	198-266	240	416	204-271	230	4.98**	105

Table 1.2. Continued.

		Spring Migration			Autumn Migration							
					Adults			Immatures				
Species	Status	n	Range	Date[A]	n	Range	Date[A]	n	Range	Date[A]	*Z*	Days[B]
Dark-eyed Junco (*Junco hyemalis*)	S	213	116-166	135	231	221-272	256	2,710	197-272	246	4.12**	121

[A]median Julian dates of passage

[B] Number of days adults occupy breeding range (difference between median dates of spring and autumn passage)

L = Nearctic-Neotropic migrant, S=Nearctic-Nearctic migrant

*P < 0.05, **P < 0.003

Appendix 1. 1. Distribution of net hours and captures of passerine species during spring at Creamer's Field Migration Station in Fairbanks AK, 1992-1998. Birds that were assumed to be breeding locally were excluded from the compilation.

	Julian Date																
Species	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131
Alder Flycatcher																	
Hammond's Flycatcher	1		1		1		2		1	1	1	1			3	2	2
Ruby-crowned Kinglet		1	3	4	2			1	2		1	1	4		1	3	
Gray-cheeked Thrush																	
Swainson's Thrush																	
American Robin							1	1	2		2	2		2	5	5	6
Orange-crowned Warbler																1	
Yellow Warbler																	
Yellow-rumped Warbler			2	24	1		2	2		1	12	4	9	6	15	19	30
Blackpoll Warbler																	
Northern Waterthrush																	
Wilson's Warbler															1	2	2
American Tree Sparrow			2	1		2	4		3	5	3	4	6	1	1	3	9
Savannah Sparrow												1		1	2	5	8
Fox Sparrow	1							3	1	1	1	3	3	3	3	3	2
Lincoln's Sparrow										1		2	1	1	2	3	5
White-crowned Sparrow									5		1	4		1	1	6	5
Dark-eyed Junco		1	1	5	2	1	9	10	4	3	5	11	11	5	5	5	10
Net Hours	1,021	1,004	1,204	976	1,214	1,047	1,532	1,530	1,348	1,330	1,582	1,598	1,329	1,623	1,534	1,516	1,489

Appendix 1.1. Continued.

	Julian Date																
	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Alder Flycatcher																	
Hammond's Flycatcher			6	3	2	1	1	7	2	2	2		3		1	3	
Ruby-crowned Kinglet	1		2	12			1	1	3		2	1					
Gray-cheeked Thrush				4		1	2	1	4	2	13	8	17	8	6	4	5
Swainson's Thrush	2	1	7	5	3	7	10	13	17	19	19	17	16	22	5	15	14
American Robin	5	5	2	14	4	8	11	7	6	4	8	8	7	11	6	2	8
Orange-crowned Warbler	1		9	10	10	7	8	17	26	15	17	9	11	12	10	6	6
Yellow Warbler				2		2		1	1	7	19	4	2	15	5	1	1
Yellow-rumped Warbler	15	14	26	82	22	54	17	24	11	12	21	18	10	19	2	7	4
Blackpoll Warbler				1	2	1	3	4	3	3	19	3	3	3		5	1
Northern Waterthrush		3	3		3	7	4	10	13	13	42	18	9	11	5	8	5
Wilson's Warbler	1		1	10	3	10	7	16	14	17	13	15	10	11	12	10	15
American Tree Sparrow	3			6	1		9	6		3		5	2	1	2	2	
Savannah Sparrow	7	2	5	9	6	10	4	3	6	10	7	26	7	13	5	5	3
Fox Sparrow	2		1	1	1		3	7	1		3	1	2	1		1	
Lincoln's Sparrow	2	2	4	3	3	2	4	1	1	3	3	1		2	4	5	1
White-crowned Sparrow	6	2	7	7	5	5	7	7		2	1	1	2	1		3	2
Dark-eyed Junco	6	1	10	7	6	3	4	23	8	8	6	2	6	8	3	4	
Net Hours	1,606	1,184	1,406	1,380	1,377	1,466	1,515	1,615	1,621	1,602	1,662	1,791	1,406	1,739	1,574	1,690	1,417

Appendix 1.1. Continued.

	Julian Date																	
	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166
Alder Flycatcher						1		8	2	3	3	1	2	9		6	1	1
Hammond's Flycatcher	1		2	1			1	1									2	1
Ruby-crowned Kinglet																		
Gray-cheeked Thrush	2	3	4	6	3		4	2		2	1							
Swainson's Thrush	10	9	12	24	10	11	1	9	3	1	1							
American Robin	4	2	3	8	4	7	5	4	4	4	8	2	4	2	1	8	2	
Orange-crowned Warbler	3	6	12	11	10	5	10	6	4	3	2		2		2	1		
Yellow Warbler	4	5	8	12	21	4	12	9	1	6	1		1	4				
Yellow-rumped Warbler	13	6		8	5	4	11	1		2	2	1			1			
Blackpoll Warbler	4			7	3		3					1						
Northern Waterthrush	4	7	2	9	18	6	4	3	1		2							
Wilson's Warbler	14	15	7	11	5	5	5	2	1	2	4			1				
American Tree Sparrow		1	1	1	1													
Savannah Sparrow	5	8	4	12	6	1	6	1			1	1	1		1	1		3
Fox Sparrow																		
Lincoln's Sparrow	4	2	2		1		3	1				1						
White-crowned Sparrow	1	1	1	1			1	2										
Dark-eyed Junco	3	3	2	3	1	3		2								1		2
Net Hours	1,795	1,220	1,276	1,735	1,312	1,377	1,155	1,751	665	1,280	1,240	401	781	741	310	805	632	623

Appendix 1.2. Distribution of net hours and captures of passerine species during autumn at Creamer's Field Migration Station in Fairbanks AK, 1992-1998. Birds that were assumed to be breeding locally were excluded from the compilation.

		Julian Date																			
		196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215
Alder Flycatcher	Adults	1	1	6		1		6		1	5	2	11	1	6	4	3	1	5	4	
	Immatures									5	4		7		10	4	3		16	10	21
Hammond's Flycatcher	Adults			1							1	3				1					
	Immatures	2	1	5	5	2		3	2	9	4	4	17	6	7	6	7	5	12	3	7
Ruby-crowned Kinglet	Adults																				
	Immatures			1				1		1		1	1	1	1						
Gray-cheeked Thrush	Adults				1																
	Immatures																1	2			
Swainson's Thrush	Adults																				
	Immatures			3							1		2		2	4		3	3	1	1
American Robin	Adults																				
	Immatures										2	1			1	1					3
Orange-crowned Warbler	Adults	1	4	2				2		1		1		1							
	Immatures	3	7	9	5	1	1	10		18	4	16	9	3	6	10	6	1	13	14	8
Yellow Warbler	Adults				2		1				1		1						1		
	Immatures	1	2		2	1	1	4		5	9	11	14	3	18	14	11		12	8	18
Yellow-rumped Warbler	Adults													1			1		1	1	
	Immatures	2	1	3	3			2			1	2	6	3	6	9	15	7	40	29	25
Blackpoll Warbler	Adults																				
	Immatures														1				1	1	3
Northern Waterthrush	Adults																				
	Immatures		1	1			1				1		3		3	2	1	1	4	3	2
Wilson's Warbler	Adults												1								
	Immatures			1	1			2		2		3	7	2	3	2	4	1	10	12	19
American Tree Sparrow	Adults																				
	Immatures																				
Savannah Sparrow	Adults			1																	
	Immatures		1	2	5			1		2	2	2	13	3	9	17	1	1	7	5	7
Fox Sparow	Adults																				
	Immatures				1														1		
Lincoln's Sparrow	Adults	1		3		1	1	2							2	1	1		2	1	
	Immatures	11	16	14	11	8	3	9	1	11	20	10	14	12	21	19	14	14	22	15	8
White-crowned Sparrow	Adults			1																	
	Immatures									1	2		1	3	11	7	12	4	7	3	2
Dark-eyed Junco	Adults																				
	Immatures		1	2		1	1	3		11	1	1	7	2		2	1	3	9	7	5
Net Hours		238	636	724	864	695	604	1,053	238	875	1,209	1,099	1,442	1,031	1,029	1,096	865	476	1,545	1,304	1,040

Appendix 1. 2. Continued

		Julian Date																		
		216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234
Alder Flycatcher	Adults	7	2	2	4				2			1				1	1		1	
	Immatures	12	14	15	26	10	13	12	15	27	21	20	14	3	9	4	5	4	6	2
Hammond's Flycatcher	Adults			1	1					1	1		2	1	1		1			
	Immatures	11	5	4	4	3	5	9	6	10	11	7	7	2	5	3	8		5	2
Ruby-crowned Kinglet	Adults											1			1	2			1	
	Immatures	1			1	2	1	2		2	3	4	3	5	13	14	10	16	17	20
Gray-cheeked Thrush	Adults										1			2		1	1		1	1
	Immatures			1	1			3	3		2		1	2	8	5	5	9	10	5
Swainson's Thrush	Adults									1	2			1	4	3		6	3	1
	Immatures	4		3	5	6	13	19	23	20	30	25	18	20	31	31	36	46	42	28
American Robin	Adults																			
	Immatures					2		1	1	3	4				1	4	4	5	3	1
Orange-crowned Warbler	Adults	1			1		1	1		2		4	2	6	5	7	3	11	8	9
	Immatures	6	3	14	18	5	28	16	35	38	47	60	55	43	115	140	73	157	204	191
Yellow Warbler	Adults	2			3			2	1	5	1	1	2		2	3	1	5	6	5
	Immatures	13	9	13	33	10	20	7	17	29	39	26	34	23	54	37	11	47	46	18
Yellow-rumped Warbler	Adults				2			1		3	3	2	1	2	3	6	3	9	10	6
	Immatures	37	32	39	36	66	117	88	107	146	177	162	210	120	195	285	163	233	220	261
Blackpoll Warbler	Adults								1				1	2	2	2		1	5	1
	Immatures		1	4	1	4	4	4	11	14	20	8	29	10	32	30	9	25	31	14
Northern Waterthrush	Adults						1				1	1	3			1	1	1	2	
	Immatures	5	1	5	10	5	6	8	5	15	11	12	13	11	16	9	6	7	10	4
Wilson's Warbler	Adults							2		1	5			2	3	1		1	7	1
	Immatures	5	4	14	23	16	22	30	15	28	41	23	21	31	88	41	17	26	51	28
American Tree Sparrow	Adults																			
	Immatures									3	1	3		1		3	1	9	8	7
Savannah Sparrow	Adults				1			2	1		2			1		3	2			
	Immatures	1	1	8	22	2	13	2	26	16	13	18	10	23	9	24	18	21	16	15
Fox Sparow	Adults													1						1
	Immatures				1		2			1	1	2	5	2	2	1	3	4	2	7
Lincoln's Sparrow	Adults				1		1	1	1	1	1				2			1	3	1
	Immatures	6	6	17	31	20	33	44	29	35	56	30	24	42	19	40	21	39	33	26
White-crowned Sparrow	Adults							1		1					1	1		1	1	
	Immatures	12	1	2	10	18	8	9	3	13	25	17	7	10	13	21	9	9	16	4
Dark-eyed Junco	Adults						1		1	2					1					1
	Immatures	8	6	1	13	12	12	14	29	25	33	46	36	20	19	48	46	58	48	44
Net Hours		1,064	511	1,006	1,145	842	1,361	1,351	1,320	1,673	1,880	1,609	1,193	1,359	1,165	1,651	1,616	1,648	1,721	1,353

Appendix 1. 2. Continued

		Julian Date																		
		235	236	237	238	239	240	241	242	243	244	245	246	247	248	249	250	251	252	253
Alder Flycatcher	Adults	2	1	1																
	Immatures	2	8	2	8	1		1	1		1	1	1			1	1			
Hammond's Flycatcher	Adults		1							1						1				
	Immatures	1	1		1	3		2	1			1	1			1				
Ruby-crowned Kinglet	Adults		1	2	3	5	1	7	3	1	1		3	4		3	2	3	4	6
	Immatures	26	9	13	14	24	33	29	32	18	50	55	23	21	20	36	11	18	10	17
Gray-cheeked Thrush	Adults	2		2		3	4	3	2	1	2	1	3	1	1	2	1	2	2	
	Immatures	7	5	8	9	14	13	13	7	9	2	7	5	5	6	6	1		3	2
Swainson's Thrush	Adults	4	6	1	4	3	5	5	3	3	5	1	6	1	2			1	1	
	Immatures	23	32	28	13	23	27	24	11	8	12	12	4	5	16	5	2		2	1
American Robin	Adults	2	1	1				1	1					1	3	2	1		2	1
	Immatures	1	5	12	1	3	5	3	12	3	2	2	4	1	5	6	4	1	3	2
Orange-crowned Warbler	Adults	14	12	6	17	17	18	28	30	53	22	47	23	19	13	38	11	12	5	16
	Immatures	84	118	188	242	192	139	109	91	86	88	131	88	73	42	66	38	45	22	23
Yellow Warbler	Adults	4	4	1	2	6	1	5	3	7	2	3	4	1	2					1
	Immatures	6	8	22	20	13	9	6	6		4	7	3	3	2	1			1	1
Yellow-rumped Warbler	Adults	8	13	11	6	10	13	19	25	20	8	26	13	7	17	18	23	12	7	7
	Immatures	128	138	306	146	143	161	243	200	119	93	137	71	69	84	174	90	99	33	52
Blackpoll Warbler	Adults	3	4	1		1	1	1	4	2								1	1	
	Immatures	12	7	8	12	3	9	17	3	2	2	1	5	1	1	4	4	1	1	2
Northern Waterthrush	Adults			1																
	Immatures	2	3	6	7	5	2	2	2	2	1	5						1	1	
Wilson's Warbler	Adults	2	3	2	1	1	6	5	4	7	1	3	2		1	2	1			
	Immatures	14	11	22	65	9	8	9	8	12	8	31	6	2	1	5				1
American Tree Sparrow	Adults		1		1		1	4	3	14	7	10	7	10	10	10	8	4	6	41
	Immatures	16	24	21	13	34	39	31	43	36	39	105	60	77	85	74	58	91	97	156
Savannah Sparrow	Adults	2	1	1		1			1	1					1	1		1	1	
	Immatures	16	16	8	14	16	10	28	6	7	4	12	9	13	6	1	1		2	7
Fox Sparow	Adults	2	4		2	1	5		2	2	2	3	3	5	8	3	3		2	3
	Immatures	4	16	7	15	8	4	12	7	2	4	16	11	9	10		5	6	3	3
Lincoln's Sparrow	Adults	3	2	3		2	4	3	2				2	2	1	2				
	Immatures	29	29	23	20	17	24	33	17	13	14	32	22	15	25	13	8	15	5	16
White-crowned Sparrow	Adults	1	1	2	1	1	6	5	2	2	2	1			1					
	Immatures	16	14	7	11	8	18	13	13	7	4	3	7	2	1	7	2	2		1
Dark-eyed Junco	Adults	1	1	2	3	5	1	1	4	4	7	5	5	6	9	6	4	4	3	7
	Immatures	58	70	41	41	57	58	72	87	59	65	99	90	79	136	95	62	63	60	91
Net Hours		1,435	1,342	1,462	1,187	1,401	1,303	1,572	1,462	1,450	1,004	1,317	1,521	1,293	1,844	1,716	1,532	1,084	1,211	1,570

Appendix 1.3. Continued

		Julian Date																	
		254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270	271
Alder Flycatcher	Adults																		
	Immatures		1	1															
Hammond's Flycatcher	Adults						1												
	Immatures																		
Ruby-crowned Kinglet	Adults	9	3	5	3	1	9	5	3	4	1	2	1	3	1	2	1		
	Immatures	46	9	25	21	11	55	42	10	6	4	11	3	9	5	4	3		1
Gray-cheeked Thrush	Adults						1		1		1		2						
	Immatures	1	2			1		2	1										
Swainson's Thrush	Adults	1	2	1		1		1	1					2				1	
	Immatures		1	1	1			2			1					1			
American Robin	Adults	3	4	2	1				1		3	1	6	9		2	11	17	1
	Immatures		1	2	1	1		3	6	5	7	3	17	26	1	1	2	9	
Orange-crowned Warbler	Adults	32	9	18	11	6	16	2	2	3	3	1	3	2					
	Immatures	43	17	18	11	6	13	3	4	1	2		1	1				1	
Yellow Warbler	Adults	1		1								1							
	Immatures						1	1											
Yellow-rumped Warbler	Adults	17	1	9	1	3	5	3	5		3		3	5		3			
	Immatures	178	25	56	22	6	23	4	11	1			1	2					
Blackpoll Warbler	Adults			1							1			1					
	Immatures	3	3	1															
Northern Waterthrush	Adults																		
	Immatures																		
Wilson's Warbler	Adults		1	2	1		7	1	1	1	3	3	3	1					1
	Immatures	2	2				2	1	2		4			1				2	1
American Tree Sparrow	Adults	44	10	65	18	28	7	40	33	16	17	12	18	6	6	8	9	26	1
	Immatures	363	41	294	287	132	55	251	168	105	75	24	133	25	25	54	3	29	3
Savannah Sparrow	Adults	2		1									1			2			
	Immatures	11	1	2	1		1	1	2			1	2			1		1	
Fox Sparow	Adults	7		1	2			1				1							
	Immatures	11	5	3	6	2	3	3	2	1	3	1	2			1	1		
Lincoln's Sparrow	Adults		1				2							1		1	1		
	Immatures	17	8	12	4	4	13	7	8	3	1		2	1	1		1	2	
White-crowned Sparrow	Adults		1			1			1			1		1					
	Immatures	1	2	2	4		4	1	1	1			2		1				1
Dark-eyed Junco	Adults	18	1	14	10	14	23	17	9	8	4	7	5	3	2	7	3	1	
	Immatures	128	35	91	83	87	26	61	84	27	29	20	28	8	3	28	5	4	
Net Hours		1,374	949	1,554	1,286	1,313	865	1,312	1,085	964	888	784	1,344	696	702	792	728	321	688

Appendix 1.3. Among-year variation in median Julian dates of passage during spring migration in Fairbanks, Alaska (1992-1998).

	1992		1993		1994		1995		1996		1997		1998		
	Median Date	n	Median Date	n	Median Date	n	Median Date	n	Median Date	n	Median Date	n	Median Date	n	*KS*, df=6
Swainson's Thrush	150	23	143	37	143	52	146	45	147	71	149	23	143	32	12.18
American Robin	149	27	141	29	142	21	146	34	146	25	142	27	139	54	5.94
Orange-crowned Warbler	151	38	140	46	142	39	146	42	149	26	150	18	143	43	7.02
Myrtle Warbler	144	105	137	93	133	41	132	78	144	74	138	62	135	86	19.22 **
Wilson's Warbler	148	33	144	54	142	55	146	57	146	16	147	13	141	14	8.61

KS = results from Kruskal-Wallis one-way analysis of variance

**P<0.01

Appendix 1. 4. Among-year variation in median Julian dates of passage (adults only) during autumn migration (15 July to 30 September) in Fairbanks, Alaska (1992-1998).

	1992		1993		1994		1995		1996		1997		1998		
	Date	n	Date	n	Date	n	Date	n	Date	n	Date	n	Date	n	*KS*, df=6
Ruby-crowned Kinglet	247	5	256	9	241	14	249	10	259	31	251	25	252	13	8.44
Orange-crowned Warbler	247	44	242	82	241	80	243	111	254	67	247	120	243	78	8.17
Myrtle Warbler	249	22	234	7	242	55	239	47	248	60	247	73	245	93	12.59
Yellow Warbler	238	9	242	20	236	11	233	30	230	6	233	10	239	8	4.64
Wilson's Warbler	263	5	245	21	240	19	243	17	259	11	233	7	242	6	9.20
American Tree Sparrow	263	31	253	110	256	46	258	120	256	42	254	71	260	58	1.95
Dark-eyed Junco	247	7	253	15	260	19	254	40	259	53	252	40	256	56	6.53

KS = results from Kruskal-Wallis one-way analysis of variance

no values were considered significant (P>0.05)

CHAPTER 2 - SEASONAL DIFFERENCES IN FAT STORES AMONG HIGH-LATITUDE PASSERINE MIGRANTS

ABSTRACT

We examined fat stores in passerine migrants at a high-latitude site in Fairbanks, Alaska (64°50' N, 147°50' W) during spring and autumn from 1992 to 1998. Our objective was to determine fat deposition patterns during the initial (autumn migration) and the final (spring migration) stages of long-distance migration. Our analyses examined factors affecting daily fat scores during migration and compared between-season differences in fat stores in 19,999 individuals of 16 migrant species. In autumn, adults had significantly higher fat scores than immatures in 12 of 16 species. However, in most species the differences observed were attributable to the effects of overnight low temperature, day length, and time of day, rather than age effects. In Swainson's Thrushes (*Catharus ustulatus*) and Yellow-rumped Warblers (*Dendroica coronata*), age effects were significant when covariates were held constant. Fat scores were higher in autumn than spring in 7 of 16 species, but these differences were due to daily environmental conditions rather than season in all but species but Swainson's Thrush, American Robin (*Turdus migratorius*), and Fox Sparrows (*Passerella iliaca*). No species arrived at this study site with high fat loads in spring, suggesting that the species examined do not carry additional fat stores to initiate breeding in this region.

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INTRODUCTION

Long-distance migration is energetically expensive (Berthold 1975, Blem 1990). For example, metabolic rates for some passerines during migration are estimated to be 6-8 times the normal resting metabolic rate (Hussel 1969). These energetic demands are satisfied by passerines through the deposition of fat stores before and during migration (e.g., Nisbet et al. 1963, Mueller and Berger 1966, Berthold 1975, Cherry 1982, Blem 1990). Despite this documentation of fat deposition at stopover sites, continental patterns of fat deposition in Nearctic-Neotropic migrants are not well understood. Understanding the geographic and temporal patterns of acquisition of the fat required for migration could elucidate broad patterns of migration strategies and the selective pressures associated with continental migration systems.

Fattening strategies employed during migration vary among species in the rate of fat deposition and the amount of fat stored (e.g., Winker et al. 1992, Winker 1995, Pilastro and Spina 1997) and may be influenced by body size, foraging habits, season (King et al. 1963, Winker et al. 1992a), and distances between breeding and nonbreeding ranges (Berthold 1996, Sandberg 1996). Further, fat deposition patterns may vary based on the location of the stopover site relative to the migrant's ultimate destination (Farmer and Wiens 1999).

Fat stores of passerines vary in response to daily environmental variables (Blem 1990) including temperature (Bednekoff et al. 1994) and photoperiod (Bednekoff and Krebs 1995). During migration, many passerines increase fat stores during the daylight hours (Cherry 1982, Blem 1990, Winker et al. 1992b, Winker 1995). Additionally,

seasonal differences in fat reserves are partly endogenously programmed in circannual patterns (Gwinner 1990). For example, some migrants undergo hyperphagia, the principle mechanism of premigratory fattening, at predictable times in the annual cycle (Berthold 1975).

High fat stores in spring relative to other times of the year have been documented in Manitoba (Biermann and Sealy 1984), Washington (King et al. 1963), and in Minnesota (Winker et al. 1992a). Additionally, passerines arrive at some high-latitude breeding ranges with high fat levels (Sandberg 1996, Fransson and Jakobsson 1998). Fat stores in passerines can provide enough energy to maintain birds during mornings when food availability is scant (Ketterson and Nolan 1978) and have been estimated to ensure survival for up to four days (Blem 1976). High fat levels upon arrival to high-latitude breeding areas may increase the probability of survival when conditions are harsher than normal and could award advantages to birds by improving reproductive success (Sandberg 1996).

The location of our study site allows us to examine the condition of Nearctic-Neotropic passerine migrants just prior to arrival upon and just after departure from high-latitude breeding grounds. Data from such locations are key to understanding geographic patterns of fat deposition among migrants through the addition of a missing piece of a complex puzzle (high-latitude information), and also enable the addressing of hypotheses developed from data collected at lower latitudes. Here we address the following working hypotheses: 1) migrants should carry relatively high fat stores during the final stages of long-distance migration (spring) to offset the possible time constraints of brief subarctic

summers and unpredictable resources early in the season; and 2) migrants should exhibit relatively lower fat levels in autumn, during the initial stages of long-distance migration, because they are presumably departing to southern regions where resources are more predictable and adverse weather conditions are less likely.

Study Area and Methods

Mist nets were operated at Creamer's Field Migration Station (CFMS), in Fairbanks, Alaska (64°50' N, 147°50'W) approximately 10 km from the confluence of the Chena and Tanana Rivers, at 130 m elevation. The Tanana Valley is well-documented migration corridor (Kessel 1984, Cooper and Ritchie 1995, McIntyre and Ambrose 1999). CFMS encompasses approximately 20 ha and provides a good representation of the common habitat types occurring within the boreal forest of interior Alaska.

Data Collection--

A standardized netting protocol was used at CFMS from 1992-1998 using an array of 22-50 standard (30 mm mesh, 2.6 m x 12 m) mist nets. The nets were arranged in a north-south direction, perpendicular to the migration corridor through the Tanana Valley. Nets were operated daily from 06:00 Alaska Daylight Savings Time to 13:00 during spring migration (25 April-15 June). During autumn migration (15 July to 30 September), net-opening times varied with sunrise (e.g., 06:00 on 15 July and 07:30 on 30 September) and closed seven hours later. Sampling at the ends of both seasons (10-15 June and 25-30 September) occurred every other day.

Birds were banded with United States Fish and Wildlife Service bands, and data were collected to determine age (autumn only, using degree of skull ossification), body mass, wing length (chord), and breeding condition (spring only). During autumn, estimates of the proportion of juvenal plumage (for immatures) were recorded.

We used ordinally scored subcutaneous fat deposits as an indicator of total body fat based based on a seven-class scoring system modified from Helms and Drury (1960): 0) no fat observed in the furculum or on the abdomen; 1) trace of fat on the furculum and abdomen; 2) thin layer of fat on the furculum and abdomen; 3) one-half furculum fat filled, fat covering most of the abdomen 4) fat in the furculum level with clavicles and slightly mounded on the abdomen; 5) slightly bulging in furculum, abdomen well mounded; 6) greatly bulging in furculum and mounded on abdomen; 7) large fat pads from where the furculum and abdomen meet. Using fat score data is a fairly precise method for indexing total body fat of passerines if observer bias is limited (Krementz and Pendleton 1990, Rogers 1991). We minimized observer bias through intensive training among field staff on thousands of birds. Although no formal measures of observer bias were recorded, staff frequently compared fat-score estimates to ensure consistency. Additionally, approximately 75% of the data were collected by 3 individuals whose tenure overlapped at the bird observatory by at least 2 years each.

Data Analysis--

We used initial captures of birds and excluded captures of individuals that were not migrants. For details see Benson (2000; Chapter 1). Because fat-score data are ordinal, we used Mann-Whitney *U*-tests to examine differences in fat levels between

spring and autumn and, in autumn, between adults and immatures. Although the median is the appropriate measure of central tendency for fat score data (Hailman 1965) the mean is also presented for comparisons with other studies that reported only means.

In addition to using ordinal fat scores, an index of body condition was calculated using mass (g) divided by wing length (mm). When body mass is standardized for body size it is a reasonable predictor of an individual's fat content in wood warblers (Rogers and Odum 1964).

Analysis of covariance (ANCOVA) was used to examine age-related differences in body condition; age was used as a main factor, and time of capture, night length, and daily low temperature (°C) were incorporated as covariates. That is, low temperature on the date the bird was captured (usually the night before), night length on the date the bird was captured (data from the Alaska Climate Research Center 2000), and time of day the bird was captured were recorded for each individual. For species with significant age-related differences in body condition, we tested for year effects using ANCOVA with year and age as main factors and time of day, daily low temperature, and night length as covariates.

Seasonal differences in body condition indices were also evaluated using ANCOVA with season as the main factor and time of capture, daily low temperature, and night length as covariates. For species with significant differences in body condition between seasons, we determined whether these differences were due to year effects by using season and year as main factors and time of day, daily low temperature, and night length as covariates in ANCOVA models. All data analyses were conducted using SPSS

(1997). Because each of these tests was conducted on 16 species, Bonferroni corrections were applied to decrease the probability of Type I statistical errors. Therefore, *P*-values less than 0.05/16 species (0.003) were considered significant.

RESULTS

Autumn fat loads--

We used both fat score data and body condition data to estimate differences in fat loads between adults and immatures in the autumn sample. Adults had significantly higher mean fat scores in 11 of 16 species (Table 2.1). Immatures did not have significantly higher fat scores in any species we examined.

When time of day, night length, and low temperature were included in ANCOVA models, age-class differences in body condition (mass/wing) were significant in only two species (Table 2.2). Age classes of both Swainson's Thrushes (*Catharus ustulatus*) and Yellow-rumped Warblers (*Dendroica coronata*) differed significantly in body condition when covariates were held constant (Table 2.2). ANCOVAs showed no interaction between age and year for Swainson's Thrush ($F_{6, 588} = 2.03$, $P = 0.073$) or Yellow-rumped Warblers ($F_{6,3324} = 0.142$, $P = 0.982$), suggesting that the age-related differences did not vary among years.

Time of day had a significant, positive effect on body condition in 11 of 16 species during autumn (Table 2.2), and negative effects were not found in any species, as expected since all birds were captured before midday. Also, in autumn, overnight low temperature had a significant effect on body condition in 3 of 16 species, and night length affected body condition in 10 of 16 species (Table 2.2).

Between-season differences in body condition--

Comparisons of fat score data (adults only) showed that 8 of 16 species had significantly higher fat loads in autumn than spring (Table 2.3). The Ruby-crowned Kinglet (*Regulus calendula*) was the only species with significantly higher mean fat scores in spring than autumn (Table 2.3). The median fat scores for all species were low, ranging from 0 (no fat visible) to 3 (one half of furculum filled with fat).

Although fat score data indicated seasonal differences in fat scores, these differences could be attributed to factors other than season in most species. When time, overnight temperature, and night length were included as covariates in ANCOVAs, three species (adults only) showed higher body condition in autumn than spring (Table 2.4). These species were Swainson's Thrush, American Robin (*Turdus migratorius*), and Fox Sparrow (*Passerella iliaca*). ANCOVA tests for interaction between season and year with time, temperature, and night length held constant showed no significant interaction (after Bonferroni corrections) for all of the following three species: Swainson's Thrush ($F_{6,262} = 2.76$, $P = 0.02$), American Robin ($F_{6,234} = 1.31$, $P = 0.26$) and Fox Sparrow ($F_{6,73} = 0.54$, $P = 0.81$). Other species examined did not show a difference in body condition that could be attributed to season alone, and no species had significantly higher body condition indices in spring when covariates were held constant.

DISCUSSION

Spring Migration Strategies--

Most species examined at our study site carry relatively low fat loads upon arrival to interior Alaska. King et al. (1965) found similar results in an intensive study on

White-crowned Sparrows in central Alaska. These findings are contrary to the results of previous studies conducted in the subarctic of Scandinavia in which some migrants arrived with high fat levels in spring (Sandberg 1996, Fransson and Jakobsson 1998).

King et al. (1965) suggested that birds may not restore the fat depleted during the final migratory flight in spring, and that the tendency to maintain increased reserves diminishes as migration progresses. While hyperphagia is well documented during and prior to migration (Berthold 1975), it is not known whether hyperphagia persists until birds reach their breeding grounds.

Birds clearly store enough fat to complete their migratory journey, but, we found no evidence that birds were carrying fat beyond what is needed for daily maintenance during spring. Perhaps birds minimize the time spent foraging and maximize the time spent migrating to arrive on the breeding grounds as early as possible. In other words, spending less time feeding and storing fat en route may provide a benefit in early arrival. Another consideration is that the amount of energy stored during spring migration is dependent on resource availability along the migration route; a bird cannot store fat for insurance if food is not readily available. Perhaps stopover sites during the final stages of spring migration do not provide sufficient resources to enable fat deposition beyond what is necessary to fuel the final stages of migration.

Autumn Migration Strategies--

Ten of sixteen species had higher fat scores in autumn than spring; however, the difference was attributable to season alone in only three species. No species had higher relative fat loads in spring than autumn. King (1965) interpreted an increase in fat

deposition prior to migration in central Alaska as premigratory fattening; however, he did not evaluate the influence of daily variables known to affect fat storage. Lower overnight temperatures and increased night length in autumn account for much of the increase in fat and body condition that we observed during this season. We could not examine the variance in food availability, but this factor may also influence fat stores (Pravosudov and Grubb 1997); and could not be ruled out as a possible mechanism for the higher fat stores we observed in autumn for three species.

Adults had significantly higher fat stores than immatures in 11 of 16 species. In many of these species, adults departed significantly later than immatures, and higher fat loads in these adults can be attributed to longer nights and colder temperatures later in the season in all but two species. Swainson's Thrush and Yellow-rumped Warblers had higher mean body condition in adults than immatures in autumn; the variation observed between age classes in these two species could not be explained by daily environmental variables.

During autumn, we expected that southward migration should provide ample resources and that the need for insurance in the form of fat stores should be less than in spring. This hypothesis was derived from most of the literature we encountered, but it does not appear valid for the species examined at this site. Moreover, the species examined did not have high subcutenous fat levels in either season. Perhaps, as King (1965) alluded, hyperphagia does not persist during the final stages of high-latitude migration in spring. Adults of most species departing from Interior Alaska appear to be

responding to energetic needs at the level of daily maintenance rather than substantial fattening for a long migratory journey.

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Table 2.1. Differences in fat scores between adults and immatures during autumn migration (15 July-30 September) at Creamer's Field Migration Station in Fairbanks, Alaska (1992-1998).

	AHY				HY				
Species	n	Mean	±SE	Median	n	Mean	±SE	Median	Z^a
Alder Flycatcher (*Empidonax alnorum*)	72	0.38	0.59	0	300	0.52	0.71	0	2.39 *
Hammond's Flycatcher (*Empidonax hammondii*)	17	0.41	0.51	0	198	0.16	0.41	0	2.68 *
Ruby-crowned Kinglet (*Regulus calendula*)	84	1.49	1.35	1	584	0.84	0.93	1	4.26 **
Gray-cheeked Thrush (*Catharus minimus*)	41	1.68	1.04	2	163	1.26	0.95	1	2.30 *
Swainson's Thrush (*Catharus ustulatus*)	77	1.77	1.12	2	602	0.93	0.96	1	7.96 **
American Robin (*Turdus migratorius*)	74	2.78	1.70	3	184	1.37	1.51	1	6.01 **
Orange-crowned Warbler (*Vermivora celata*)	437	1.59	1.39	1	2310	0.83	0.99	1	10.16 **
Yellow-rumped Warbler (*Dendroica coronata*)	254	1.39	1.40	1	3532	0.39	0.68	0	14.09 **
Yellow Warbler (*Dendroica petechia*)	68	1.57	1.53	1	508	0.77	1.06	0	4.25 **
Blackpoll Warbler (*Dendroica striata*)	32	1.56	1.22	1	254	0.85	0.94	1	3.29 **

Table 2.1. Continued.

Species	AHY				HY				
	n	Mean	±SE	Median	n	Mean	±SE	Median	Z^a
American Tree Sparrow (*Spizella arborea*)	391	2.44	1.41	3	2159	1.82	1.42	2	7.73 **
Savannah Sparrow (*Passerculus sandwichensis*)	202	1.06	1.12	1	439	0.83	1.06	0	2.46 **
Fox Sparrow (*Passerella iliaca*)	32	1.45	1.04	1	184	1.13	1.12	1	2.25 *
Lincoln's Sparrow (*Melospiza lincolnii*)	51	1.47	1.53	1	1029	1.00	1.16	1	1.70 *
White-crowned Sparrow (*Zonotrichia leucophrys*)	32	2.03	1.18	2	346	0.72	0.98	0	4.53 **
Dark-eyed Junco (*Junco hyemalis*)	176	1.85	1.53	2	1941	0.92	1.08	1	8.05 **

a. Z-values from Mann-Whitney *U*-test.
* $P < 0.05$, **P < 0.003

Table 2.2. Body condition (mass/wing chord) of adults and immatures during autumn migration (15 July-20 September) at Creamer's Field Migration Station in Fairbanks, Alaska (1992-1998). ANCOVA models were used with age class as the main factor and time of day (time), daily low temperature, and night length on the date prior to capture as covariates.

	Body Condition Index					Covariates					
	Adults		Immatures			Time		Low Temperature		Night Length	
Species	*n*	Mean	*n*	Mean	F	b	F	b	F	b	F
Alder Flycatcher	72	0.181	300	0.182	2.56	0.00066	6.21	0.00048	8.11 *	0.00291	27.22
Ruby-crowned Kinglet	84	0.115	584	0.115	0.78	0.00094	55.86 **	-0.00044	0.48	-0.00046	4.05 *
Gray-cheeked Thrush	41	0.317	163	0.313	0.45	-0.00057	0.28	0.00019	0.1	0.00277	1.50
Swainson's Thrush	77	0.318	601	0.305	28.6 **	0.00010	10.30 **	0.00034	3.07	0.00414	31.23 **
American Robin	67	0.661	176	0.635	0.12	0.00122	0.42	0.00082	1.19	0.01333	12.41 **
Orange-crowned Warbler	437	0.159	2310	0.158	0.1	0.00109	176.51 **	0.00016	11.45 **	0.00082	27.33 **
Yellow-rumped Warbler	254	0.181	3532	0.176	14.5 **	0.00095	127.37 **	0.00023	23.59	0.00211	143.75 **
Yellow Warbler	68	0.159	508	0.156	0.71	0.00114	30.27 **	0.00017	2.48	0.00227	46.89 **
Blackpoll Warbler	32	0.174	254	0.169	2.31	0.00123	14.67 **	0.00006	0.079	0.00206	7.80 *
Wilson's Warbler	73	0.140	609	0.137	2.61	0.00093	43.45 **	0.00004	0.23	0.00124	18.04 **
American Tree Sparrow	391	0.240	2159	0.240	1.6	0.00172	129.32 **	0.00018	5.01 *	0.00749	466.20 **

Table 2.2. Continued.

	Effect of age on body condition				
	Adults		Immatures		
Species	*n*	Mean	*n*	Mean	F
Savannah Sparrow	202	0.243	439	0.241	0.01
Fox Sparrow	32	0.426	184	0.419	1.4
Lincoln's Sparrow	51	0.267	1029	0.262	2.89
White-crowned Sparrow	32	0.336	346	0.327	5.41 *
Dark-eyed Junco	176	0.248	1941	0.248	5.02

*P < 0.05, **P < 0.003 (significance level with Bonferroni adjustments)

Covariates					
Time		Low Temperature		Night Length	
b	F	b	F	b	F
0.00049	1.77	0.00077	14.18 **	0.00271	22.39 **
0.00166	3.50	0.00027	9.29 **	0.00505	9.29 **
0.00098	14.53 **	0.00009	0.431	0.00076	4.21 *
0.00225	14.41 **	0.00000	0.00	-0.0003	0.09
0.00094	45.01 **	0.00016	4.25	-0.0006	103.99 **

Table 2.3. Seasonal differences in fat scores between spring and autumn (adults only) in passerine migrants at Creamer's Field Migration Station in Fairbanks, Alaska (1992-1998).

	Spring				Autumn				
Species	*n*	Mean	±SE	Median	*n*	Mean	±SE	Median	*Z*
Alder Flycatcher	39	0.15	0.43	0	72	0.38	0.59	0	2.68 *
Hammond's Flycatcher	58	0.50	0.75	0	17	0.41	0.51	0	0.12
Ruby-crowned Kinglet	46	2.30	1.53	2	84	1.49	1.35	1	2.81 **
Gray-cheeked Thrush	98	1.04	0.88	1	41	1.68	1.04	2	3.33 **
Swainson's Thrush	270	0.99	0.85	1	77	1.77	1.12	2	5.63 **
American Robin	209	0.55	0.7	0	74	2.74	1.72	3	10.30 **
Orange-crowned Warbler	234	1.23	1.32	1	437	1.55	1.40	1	4.55 **
Yellow-rumped Warbler	516	1.21	1.21	1	254	1.39	1.40	1	1.20
Yellow Warbler	139	0.71	0.95	0	68	1.57	1.53	1	3.78 **
Blackpoll Warbler	46	1.37	1.06	1	32	1.56	1.22	1	0.73
Wilson's Warbler	225	1.42	1.23	1	73	2.15	1.36	2	3.94 **

Table 2.3. Continued

Species	Spring				Autumn				
	n	Mean	±SE	Median	*n*	Mean	±SE	Median	*Z*
American Tree Sparrow	83	2.19	1.16	2	391	2.44	1.41	3	2.56 *
Savannah Sparrow	177	1.08	1.13	1	202	1.06	1.12	1	0.04
Fox Sparrow	45	1.33	1.26	1	57	1.46	1.04	1	2.25 *
Lincoln's Sparrow	67	1.03	1.22	1	51	1.47	1.53	1	1.40
White-crowned Sparrow	86	1.23	1.26	1	32	2.03	1.18	2	3.13 **
Dark-eyed Junco	206	1.64	1.43	2	176	1.85	1.53	2	1.10

a. Z-values from Mann-Whitney *U*-test.
* $P < 0.05$, **P < 0.003

Table 2.4. Differences in adult body condition (mass/wing chord) between spring (25 April to 15 June) and autumn migration (15 July-20 September) at Creamer's Field Migration Station in Fairbanks, Alaska (1992-1998). ANCOVA models were used with age class as main factors and time of capture (time), daily low temperature, and night length on the date of capture as covariables.

	Season					Covariates					
	Spring		Autumn			Time of Capture		Low Temperature		Night Length	
Species	*n*	Mean	*n*	Mean	F	b	F	b	F	b	F
Alder Flycatcher	39	0.186	72	0.181	0.81	-0.00014	0.08	-0.0009	9.12 **	-0.00074	1.55
Ruby-crowned Kinglet	46	0.117	84	0.115	0.41	0.00079	5.2	-0.0002	2.24	-0.00033	1.18
Gray-cheeked Thrush	98	0.29	41	0.317	5.48 *	0.00159	3.92	0.00082	2.85	0.00478	46.06
Swainson's Thrush	270	0.286	77	0.318	46.93 **	0.00105	4.01 *	0.00094	9.76 **	0.00609	162.00
American Robin	209	0.59	67	0.661	25.27 **	0.00247	2.72	0.00051	0.619	0.00857	30.47
Orange-crowned Warbler	234	0.155	437	0.159	5.74 *	0.00143	68.4 **	0.00052	0.4	0.00069	26.09
Yellow-rumped Warbler	516	0.176	252	0.178	3.38	0.00077	14.08 **	-0.00045	22.19 **	0.00145	58.05
Yellow Warbler	139	0.156	68	0.159	1.81	0.00118	11.4 **	-0.0002	0.596	0.00061	3.90
Blackpoll Warbler	62	0.168	32	0.174	0.06	0.00208	12.45 **	0.00079	4.64 *	0.00107	4.86
Wilson's Warbler	225	0.138	70	0.14	0.56	0.00198	62.26 **	-8E-05	0.442	0	0.00

Table 2.4. Continued.

	Season				
	Spring		Autumn		
Species	*n*	Mean	*n*	Mean	F
American Tree Sparrow	83	0.228	389	0.24	0.73
Savannah Sparrow	177	0.241	24	0.243	0.00
Fox Sparrow	45	0.397	57	0.426	13.26 **
Lincoln's Sparrow	67	0.261	51	0.267	0.15
White-crowned Sparrow	86	0.329	32	0.336	1.42
Dark-eyed Junco	206	0.242	176	0.248	3.38

*P < 0.05, **P < 0.003 (significance level with Bonferroni adjustments)

Covariates					
Time of Capture		Low Temperature		Night Length	
b	F	b	F	b	F
0.00238	44.37 **	-0.0006	12.47 **	0.00049	6.16
0.00108	3.9	-0.0002	0.2	-0.00127	0.03
0.00194	4.09 *	0.00061	1.56	0.00482	24.26
0.00069	0.837	0.00045	2.47	0.00126	3.66
0.00246	6.46 *	-0.0004	0.647	0.00214	5.04
0.00079	4.07 *	-7E-05	0.124	-0.00073	28.48

CHAPTER 3 - OVERLAP OF MOLT AND MIGRATION AMONG HIGH-LATITUDE PASSERINE MIGRANTS

ABSTRACT

The temporal constraints upon birds to complete breeding and prebasic molt are most severe on populations breeding at high latitudes. We examined whether temporal constraints at high latitudes cause some passerine migrants to complete molt during autumn migration. We also evaluated energetic costs, in terms of fat loads, of overlapping these two energetically demanding events. Data were collected on molt and subcutenous fat stores at a banding station in Fairbanks, Alaska (64°50' N, 147°50'W) during autumn migration (1992-1998). In six of seven species examined, 10-54% of individuals were in the late stages of remex molt during final species-level migration periods. Of the seven species examined, only Wilson's Warblers (*Wilsonia pusilla*) did not overlap remex molt with autumn migration at this site. In five of the seven species, birds molting remiges had significantly lower fat levels than birds that had completed remex molt. Because fat stores are used to fuel migration, molt overlap does appear to impose a cost. While lower fat levels may compromise the initial stage of migration, the consequences of this likely cost are unknown.

[1] Prepared for submission in *The Auk* as Benson, A. M. and K. Winker. Overlap of molt and migration among high-latitude passerine migrants.

INTRODUCTION

Molt is energetically costly because of increased metabolic requirements for the production of new feathers and a reduction in effective insulation (Payne 1972). Molt is also costly in terms of time; the briefest estimates of the duration of molt in passerines range from 35 to 45 days (Morton et al. 1969, Rimmer 1988, Vega Rivera et al. 1998). Because migration is also energetically costly (Berthold 1975, Blem 1980) it is usually temporally separated from molt (Payne 1972, Cannell et al. 1983, Vega Rivera et al. 1998) to stabilize energetic demands on individuals (Kendeigh 1949). However, few studies have outlined the temporal partitioning of breeding, molt, and migration in Nearctic-Neotropic passerine migrants (but see Rimmer 1988, Vega Rivera et al. 1998).

The overlap of molt and migration must have energetic costs (e.g., Lindström et al. 1994), but it has been documented in some passerines: Rose-breasted Grosbeaks (*Pheucticus ludovicianus*; Cannell et al. 1983), Rough-winged Swallows (*Stelgidopteryx serripennis*; Yuri and Rohwer 1997), Yellow Warblers (*Dendroica petechia*; Rimmer 1988), and several other species (Winker et al. 1992). The pressure to overlap energetically costly events such as migration and molt is presumably highest where the duration of predictable resources is briefest. Subarctic summers are brief, and migrants occupy high-latitude breeding ranges for relatively brief periods (Benson 2000, Chapter 1). If Nearctic-Neotropic migrants respond to temporal constraints by overlapping molt and migration, this overlap should be at an extreme among populations breeding at the highest latitudes of a species' range.

We examined the temporal overlap of molt and migration in passerine migrants at a high-latitude site in interior Alaska. We also examined the hypothesis that molting during migration imparts a cost, in terms of lower fat levels, compared with birds that do not overlap molt and migration.

Study Area and Methods

Mist nets were operated at Creamer's Field Migration Station (CFMS), in Fairbanks, Alaska (64°50' N, 147°50'W). CFMS spans approximately 20 ha and includes the common habitat types locally available in the boreal forest. Our standardized netting protocol used an array of 22-50 standard (30 mm mesh, 2.6 m x 12 m) mist nets operated daily beginning at sunrise and closing seven hours later from 15 July to 25 September and every other day from 26 to 30 September (1992-1998).

We studied species in which adults undergo a complete prebasic molt (Dwight 1900). Because immatures do not undergo a prebasic molt prior to migration from high latitudes (Dwight 1900), we excluded them from these analyses. All individuals were aged using degree of skull ossification. We included only first captures of birds and we excluded birds that may have bred locally (females with incubation patches and birds recaptured more than 7 days after their first capture). Although some birds captured may have bred locally at our study site, the proportion of these birds in the sample must be small. The number of birds captured during the breeding season is extremely small when compared with the vast numbers that move through during peak migratory periods. After removal of known or suspected local breeders, we assumed that the vast majority of the birds in subsequent analyses were migrants.

The intensity of remex molt was scored by the number of primaries and secondaries growing or completely grown, and based on the assumption that these feathers were molted in standard sequence (Dwight 1900). Primaries were numbered 1-9 (or 10 depending on the species) distally from the carpal joint, and secondaries were numbered 1-6 proximally from the carpal joint (Dwight 1900). Individual feathers were scored 0 if they had not molted, 1 if they were growing, and 2 if they were completely grown. The sum of the growing and completely grown remiges was used to calculate a molt score for every individual. For example, in species with 10 primaries and 6 secondaries the molt score of an individual that had completed molt was 32. We grouped birds according to stage of remex molt based on four categories: early (remex molt 1-33% completed); mid (34-66% completed); late (67-99% completed); and complete (remex molt complete; i.e., primaries and secondaries replaced).

Extent of body molt was determined by examining the bases of the contour feathers on the bird's body and was classified based on a four-class scoring system: 0 (no body molt); 1 (light body molt; less than 1/3 of contour feathers molting); 2 (medium body molt; from 1/3 to 2/3 of a bird's contour feathers molting); and 3 (heavy body molt; more than 2/3 of the feathers molting). Body molt occurs simultaneously with remex molt. Consequently, remex molt alone has been used as an index for the entire prebasic molt (e.g., Rimmer 1988). We compared stage of body molt with remex molt intensity (based on the number of primaries or secondaries molting) using Spearman rank correlations. There was a significant relationship between body molt and remex molt intensity among individuals of the three most abundant species examined: Orange-

crowned Warbler (*Vermivora celata*; $r_s = 0.67$, $P < 0.001$, $n = 315$); Yellow-rumped Warbler (*Dendroica coronata*; $r_s = 0.51$, $P < 0.001$, $n = 163$); and Dark-eyed Junco (*Junco hyemalis*; $r_s = 0.60$, $P < 0.001$, $n = 154$). The less common species were not tested in this manner; however, this strong relationship between body and remex molt justifies our use of remex molt alone as an index of the prebasic molt, and body molt data are not considered further.

At the species level, overlap of molt and migration was defined as the percentage of individuals molting during peak species-level movements. Peak migratory periods were calculated using the median date of adult passage (Benson 2000, Chapter 1). We adjusted each capture for year effects by using annual median dates of passage for that species (Benson 2000; Chapter 1, Appendix 1.4). "Period 1" was defined as 6-15 days prior to median date of adult passage, "Period 2" was the median date of passage $\pm$ 5 days, and "Period 3" was 6-15 days after the median date of adult passage. We included a fourth period of 10 days only for species in which individuals were captured more than 15 days after median dates of passage. None or very few individuals were captured after Period 3. Ten day periods were used because low sample sizes in some species prevented a more refined grouping. The temporal overlap of molt and migration was quantified only in species for which at least 30 adults were examined.

Birds captured in the third migratory period were likely migrating because these captures represent the latest documentation of these species in interior Alaska. That is, mist nets were operated until species was no longer detected in interior Alaska. Birds captured in the first and second migratory periods were also likely migrants because we

removed all birds that had indications that they may be breeding locally, and the numbers of birds captured during the migratory periods was much higher than the captures of birds early in the fall netting period.

We used observations of subcutaneous fat deposits as indicators of total body fat based on a seven-class scoring system modified from Helms and Drury (1960); for details see Benson (2000; Chapter 2). Fat scores of molting and nonmolting birds were compared using Mann-Whitney *U*-tests. We did not use body condition indices (e.g., mass/wing) in these analyses because body mass varies during molt in relation to the numbers of feathers growing (King et al. 1965, Holmes 1966, Newton 1968, Evans 1969, and Myrcha and Pinowski 1970). For example, mass increase due to molt has been documented as 8% of the average body mass for White-crowned Sparrows (*Zonotrichia leucophrys*) in interior Alaska; this seems to occur because of follicular enlargement, growth of papillae, and an overall increase in blood volume (King et al. 1965).

RESULTS

Overlap of molt and migration--

Adults of 7 species (n = 1,018) were examined for remex molt and fat score. The percentage of birds captured that were molting ranged from 11% of Wilson's Warblers (*Wilsonia pusilla*) to 63% of Yellow Warblers (*Dendroica petechia*; Table 3.1). In Ruby-crowned Kinglets (*Regulus satrapa*), Yellow Warblers, Yellow-rumped Warblers (*Dendroica coronata*), and Dark-eyed Juncos (*Junco hyemalis*) high proportions of individuals were molting early in the migratory period, but relatively low proportions of birds were molting in the second and third periods (Figure 3.1). In Orange-crowned

Warblers (*Vermivora celata*), Wilson's Warblers, and American Tree Sparrows (*Spizella arborea*), lower than 10% variation occurred in the proportion of individuals molting in each migratory period (Fig. 3.1).

In 6 of 7 species examined, large proportions of individuals captured were in the late stages of remex molt during the final species-level migration period (Fig. 3.1). The percentage of individuals molting remiges during the final species-level movements varied among species. Although sample sizes in these periods are small, remex molt was still occurring in 14% of Ruby-crowned Kinglets, 30% of Orange-crowned Warblers, 53% of Yellow Warblers, 35% of Yellow-rumped Warblers, 10% American Tree Sparrows, and 50% of Dark-eyed Junco's. Remex molt was completed in all Wilson's Warblers 6-15 days past peak species-level movements (Fig. 3.1). Further, remex molt was completed in approximately 90% of Wilson's Warblers during early and peak species-level movements (Fig. 3.1).

Fat deposition during remex molt--

Birds that had completed remex molt had significantly higher fat levels than birds that were in the late stages of remex molt in 5 of the 7 species examined (Fig. 3.2), including Orange-crowned Warblers, Yellow-rumped Warblers, Wilson's Warblers, American Tree Sparrows, and Dark-eyed Juncos. No molting individuals of any species had higher fat levels than birds that had already completed molt.

DISCUSSION

Overlap of molt and migration occurred in 6 of 7 species examined at our study site. In some species, the overlap of molt and migration was more pronounced than

others. For example, more than 50% of Yellow Warblers were still molting throughout the migratory period. This is in stark contrast from Wilson's Warblers, which showed almost complete segregation of remex molt and migration, that is, none of the individuals captured in the final migratory period were molting, and only small proportions of the birds captured during the first and second periods were molting. For the segregation of molt and migration to be possible, Wilson's Warbler's may take less time to molt or breed compared with other species examined. We did not attempt to quantify interspecific differences in the duration of molt, nor did we have data on nesting chronology to explore these possible explanations.

Among-species comparisons in the timing of migration and the degree of molt-migration overlap showed that fewer individuals overlapped molt and migration in species that departed later. Ruby-crowned Kinglets and American Tree Sparrows were two of the latest species to migrate through the study site during autumn (Benson 2000; Chapter 1) and 10-14 % of these two species were still molting during the last migratory period. Similarly, 30-35% of Orange-crowned-Warblers and Yellow-rumped Warblers captured in the final migratory period were still molting, and the departure dates of these two species are in the middle range of species examined at this site (Benson 2000; Chapter 2). Finally, compared with other species, Yellow Warblers had the highest percentage of individuals still molting during the final species-level movements (53%) and this species departs approximately 10 days earlier than Orange-crowned Warblers and Yellow-rumped Warblers.

The briefest duration of passerine molt ranges from 35 to 45 days (e.g., Morton et al. 1969, Rimmer 1988, Vega Rivera et al. 1998). The Yellow Warbler not only departs from this region early in autumn; it also arrives later in spring compared with other species (Benson 2000), suggesting comparatively tight time limits available for reproduction and molt. It may not be possible to accelerate the duration of molt and, perhaps, species that occupy their breeding ranges for the briefest periods may tend to have the greatest molt-migration overlap.

Birds that migrate while completing the later stages of remex molt could be at a disadvantage because they stored less fat than birds that had completed molt. Because fat powers migration (Berthold 1975, Blem 1980), lower fat levels during the initiation of autumn migration at high latitudes may result in fitness costs. Overlap of molt and migration has also been documented at other high-latitude sites (e.g., Rimmer 1988, Swensson and Merilä 1996), however, there is no ready explanation for the among species variation in the degree of molt-migration overlap.

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Figure 3.1. Overlap of remex molt and migration during 10-day migratory periods. Ten-day periods are based on median dates of passage of adults (Benson 2000) and corrected for year. See text for details.

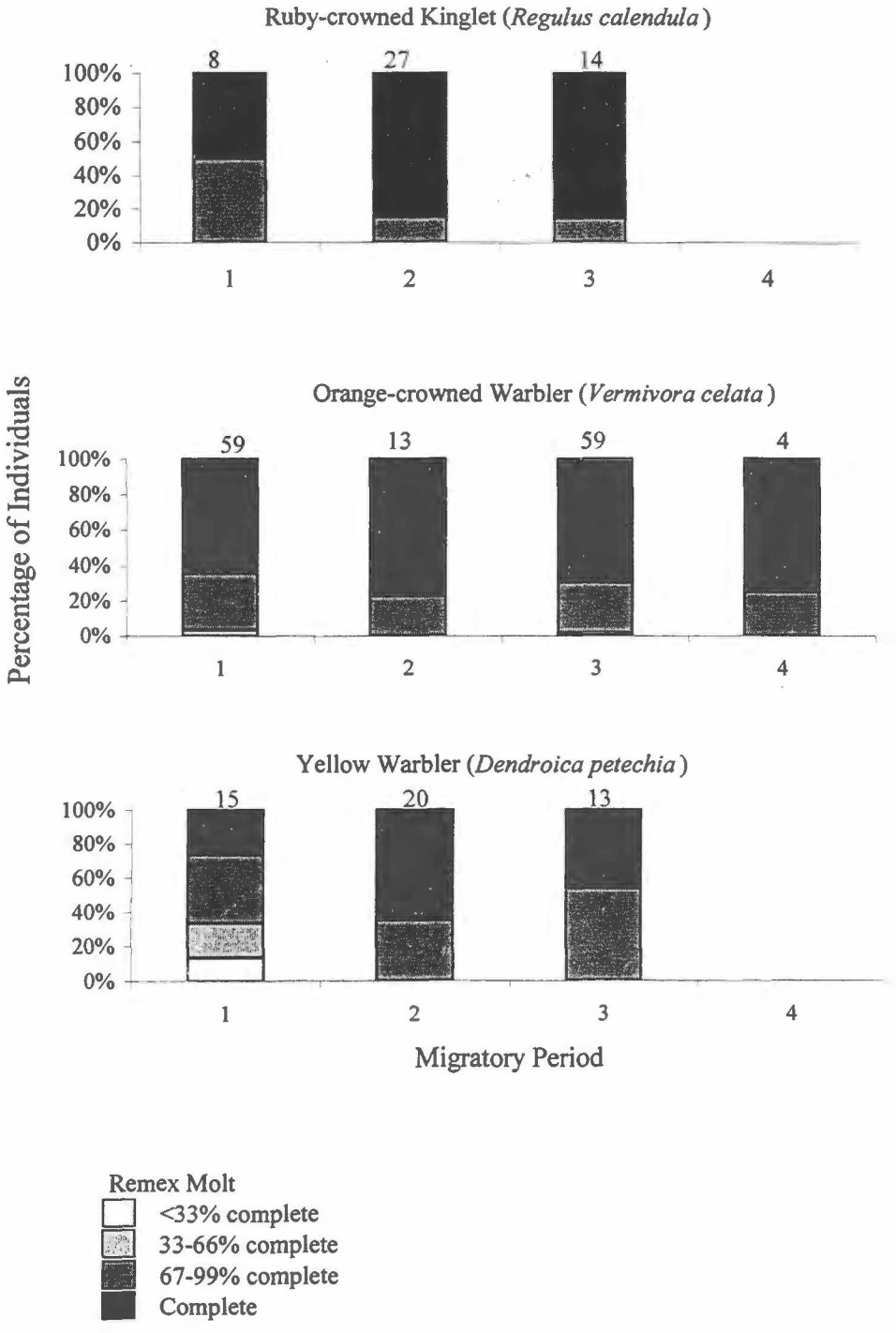
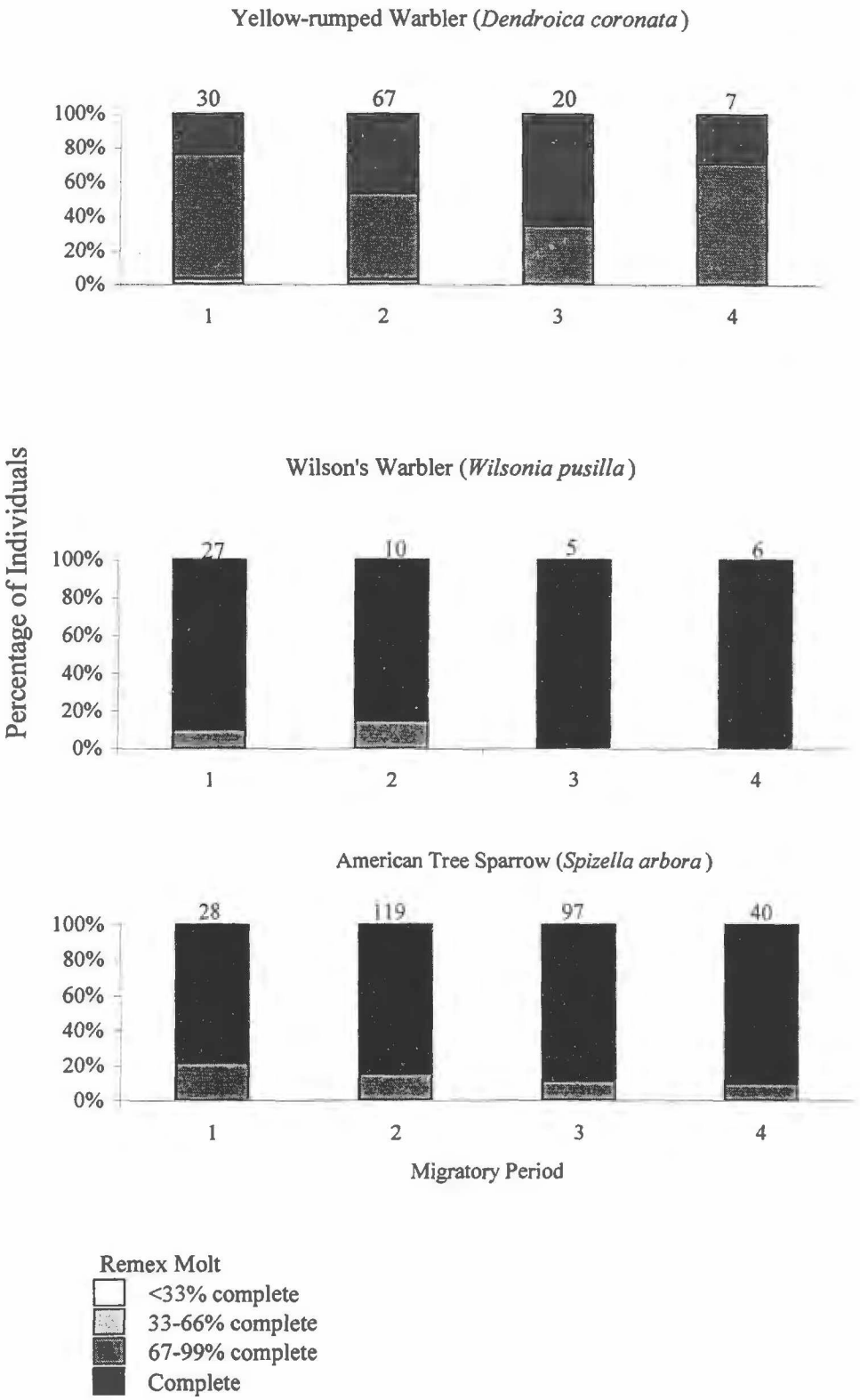


Figure 3.1. Continued.



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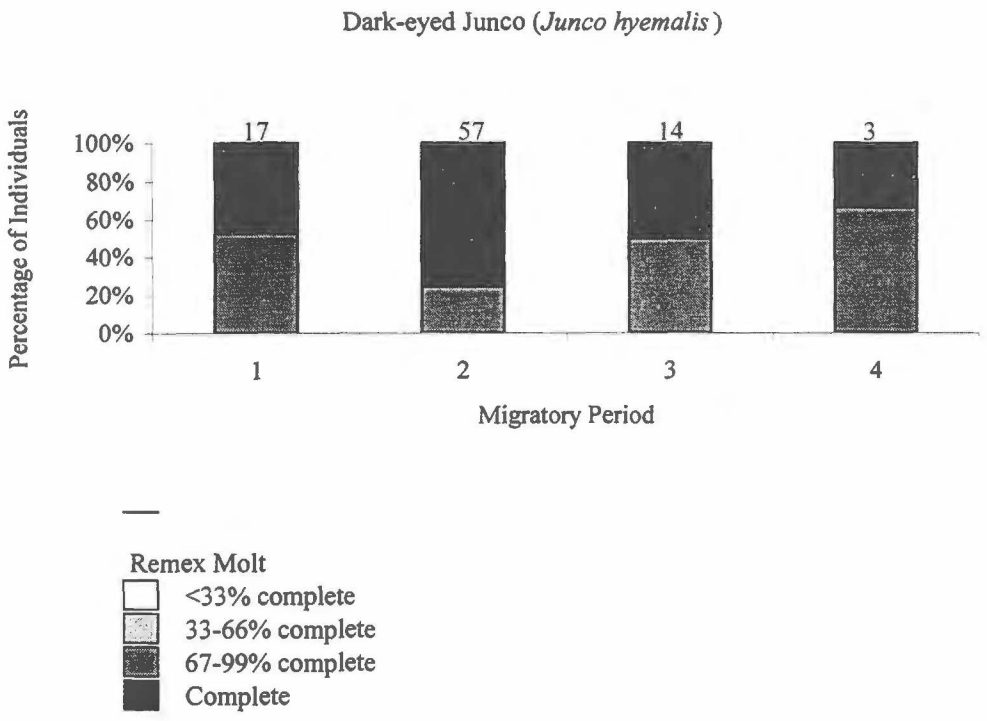
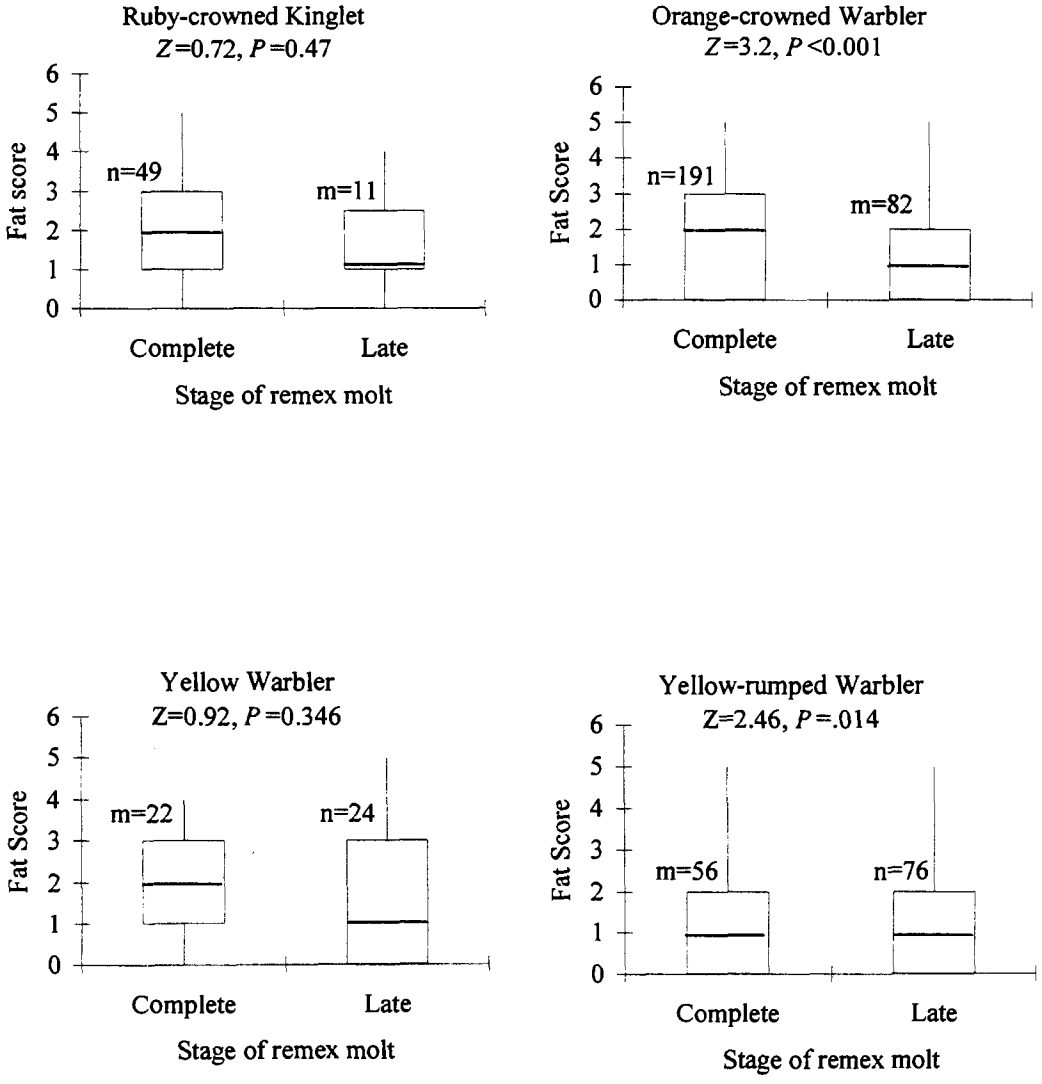


Fig. 3.2. Differences in fat scores between birds with complete remex molt and birds in the late stage of remex molt (67-99% complete remex molt). Box plots display the median (horizontal line within boxes), the interquartile range (extent of boxes), and the range of fat scores (vertical lines from boxes). Z- and P-values represent results from MW test comparing fat scores between molting nonmolting birds.



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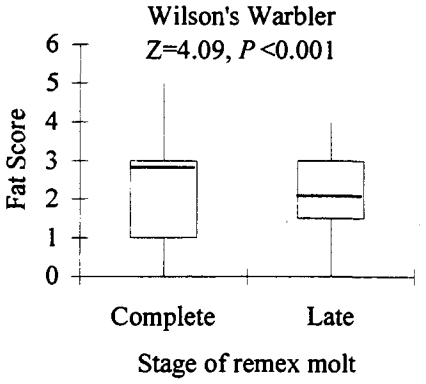

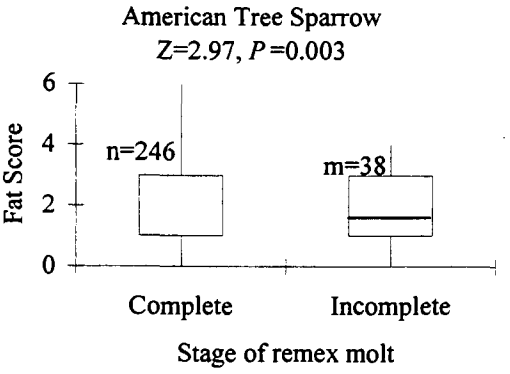

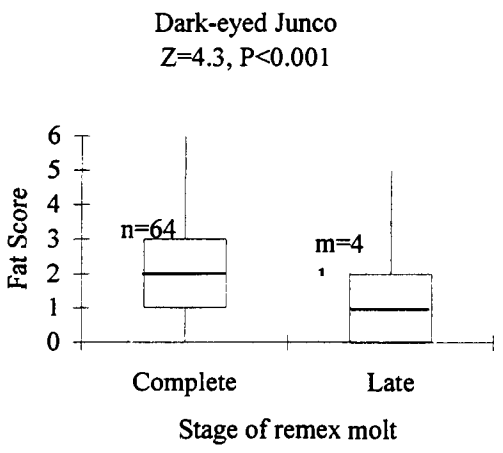

Table 3.1. Number of individuals molting compared with total number of captures.

Species	N	Number molting	% Molting
Ruby-crowned Kinglet	50	25	50
Orange-crowned Warbler	283	92	33
Yellow Warbler	60	38	63
Yellow-rumped Warbler	143	87	61
Wilson's Warbler	55	6	11
American Tree Sparrow	286	39	14
Dark-eyed Junco	141	77	55
Total	1,018		